Soil organic matter accumulation and its implications for nitrogen mineralization and plant species composition during succession in coastal dune slacks

Berendse, F.; Lammerts, E.J.; Olff, H.

Published in:
Plant ecology

DOI:
10.1023/A:1008051931963

Plant Ecology **137:** 71–78, 1998.

Soil organic matter accumulation and its implications for nitrogen mineralization and plant species composition during succession in coastal dune slacks

F. Berendse, E. J. Lammerts* & H. Olff
*Nature Conservation and Plant Ecology Group, Department of Environmental Sciences, Wageningen Agricultural University, Bornse steeg 69, NL-6708 PD Wageningen, The Netherlands; * Ministry of Agriculture, Nature Conservation and Fisheries, Mieddijk 2, NL-9036 LD Menaldum, The Netherlands*

Received 9 June 1997; accepted in revised form 10 March 1998

Key words: Dune slacks, Nitrogen mineralization, Plant species replacement, Soil organic matter accumulation, Succession

Abstract

Vegetation and soil development during succession in coastal dune slacks on Terschelling island, the Netherlands, was investigated, by comparing neighbouring ecosystems on similar substrates that had been developing for 1, 5, 35 and 76 years since the vegetation and organic soil layer had been removed. In this successional sequence, soil organic matter accumulated rapidly due to the production of litter and dead roots. N mineralization was extremely low, increasing from 0.2 g m^{-2} yr^{-1} after 5 years to 0.8 g m^{-2} yr^{-1} after 76 years. It was accompanied by a decline in the pH (KCl) in the upper 10 cm of the soil from 6.8 to 4.4. Most of the above-ground biomass accumulated in the shrub species *Oxycoccus macrocarpos* and *Salix repens*. The 5- year-old plots harboured many plant species (18 species per 0.25 m^2), but plant species diversity was much lower in the older plots. It is concluded that most changes in species composition and the decline in diversity occurred because early successional plant species were gradually outshaded by the thick litter layer and the accumulated shrub biomass.

Introduction

The supply of nitrogen and other plant nutrients is one of the most important environmental factors determining the dynamics of species composition in many ecosystems (e.g., Tilman 1988; Berendse and Elberse 1990). During early succession the amount of organic matter and nitrogen in the soil increases due to the production of litter and dead roots (Crocker and Major 1955; Olson 1958; Berendse 1990). In a chronosequence of plots in dry heathlands we found that nitrogen mineralization rose from 1 to c. 13 g N m^{-2} yr^{-1} over a period of about 50 years, as a result of the accumulation of soil organic matter (Berendse 1990). Concomitantly, soil moisture increased, whereas soil pH declined sharply. Such changes in soil features can be expected to have an important impact upon the establishment and competitive ability of plant species and ultimately upon the dynamics of the species composition of the plant community. During succession in many Western European heathlands perennial grasses such as *Molinia caerulea* and *Deschampsia flexuosa* replace the ericaceous dwarf shrubs *Calluna vulgaris* and *Erica tetralix* after a number of years, while the diversity of plant species declines. In experiments where we retarded or accelerated the rate of soil organic matter accumulation we found evidence that this change in species composition is caused by the sharp increase in nitrogen mineralization that occurs during succession (Berendse et al., 1994).

This paper reports a study to investigate whether the mechanism that we proposed as driving succession in heathlands has more general significance. It involved reconstructing the succession in moist dune valleys by describing the soil and vegetation in four neighbouring sites on identical substrates, in which the ecosystem had been developing for 1, 5, 35 and 76 years, respectively. In the three younger sites, succession had started after the vegetation and the organic soil layer had been removed for nature conservation purposes. In the oldest site, succession had started after the incursion of sea water in 1915 had washed away most of the vegetation and soil organic matter. In this chronosequence of four succcessional phases we reconstructed the accumulation of soil organic matter and the resulting changes in N mineralization, soil moisture, soil pH, plant biomass and plant species composition.

Study site and methods

Study site

The study site (53°24′ N, 5°C20′E) was located in the coastal dunes of Terschelling island in the Netherlands which is part of the northern chain of small islands between the Wadden Sea and the North Sea. The site is part of the largest secondary dune valley on the island, which was blown out between 1825 and 1865 (Van Dieren 1934). At that time the area was separated from the sea by a low ridge of blown sand. In 1915 the sea breached this ridge and inundated most of the site (Westhoff and van Oosten 1991). From then the northern dune ridge was carefully managed and undisturbed vegetation development started. In the twenties the area was still sparsely vegetated; at that time the salt-tolerant annual *Centaurium littorale* was observed to be the most frequent plant species. This species is typical of very early successional phases on primary beach plains. In 1937 the vegetation consisted of plant communities dominated by *Schoenus nigricans* (Westhoff and Van Oosten 1991).

In 1956 the vegetation and the litter and humus layer were removed in a patch of ca. 500 m^2 in order to restore the early successional vegetation, that harboured many rare plant species such as *Schoenus nigricans* and *Parnassia palustris*. In 1986 and 1990, turf was stripped from areas of about 5000 and 6000 m^2, respectively, for the same reason. In the 1986 sites the abundance of each plant species was recorded immediately before turf removal. In 1991 the species composition of the vegetation in the areas where no soil organic matter and vegetation had been removed was very similar to what had been recorded in the 1986 plots prior to turf removal.

We marked out plots of 25 × 20 m in the 1956, 1986 and 1990 sites and in the area that had been undisturbed since 1915. The plot in the 1915 site was surrounded by the 1956 and the 1986 sites. All plots were located within an area of 150 by 50 m. The substrate was very homogeneous and consisted of aeolian sand deposits. Groundwater levels were very high. During the winter period most of the area was waterlogged. In each plot five subplots of 5 by 5 m were laid out in which the soil and vegetation samples were taken.

Soil organic matter and N mineralization

On 6 August 1991 ten soil cores (diameter 7 cm) were taken in each of the four plots (two samples per subplot) to a depth of 10 cm below the boundary between the L and the FH layers and from 10 to 20 cm. The samples were subdivided into the loose litter (L), the humus layer (FH) and the underlying mineral soil (M). One of each pair of samples was used to measure organic matter and nitrogen contents in the soil, and the other sample was used to measure the root biomass in the various soil layers (cf. next section). The soil in each first sample was dried at 105 °C, weighed and ground. The organic matter content was determined as the loss of mass upon ignition (650 °C, 2 h). Total N contents were measured using a Heraeus CHN-RAPID elemental analyser.

The net mineralization of nitrogen was measured *in situ* during 6 periods of about 8 weeks: from 29 October 1991 to 21 January 1992, from 21 January to 17 March, from 17 March to 11 May, from 11 May to 7 July, from 7 July to 1 September and from 1 September to 27 October 1992. On each sampling date ten pairs of soil cores were taken in each plot (two pairs per subplot). They were taken with a 4.3 cm diameter polyvinyl chloride tube so that the sample was an undisturbed column of the first 10 cm of soil. Depth was measured from the top of the FH layer. One of each pair of samples was transported to the laboratory in a cooled box and extracted within 24 h. The other tube was incubated *in situ* after being closed with plastic lids that prevented water moving through the tube, but allowed air to enter through holes that remained above the soil surface during incubation. After the field incubation the incubated soil tube was also taken to the laboratory. There, the soil in the retrieved tubes was mixed and 20 g field-moist soil was extracted with 50 ml 1 *N* KCl. The extract was analysed for NH_4^+ and NO_3^- using an autoanalyzer. Net N mineralization was calculated as the difference between the NH_4^+-N plus NO_3^--N content of the incubated sample and its paired initial sample, whereas net nitrification was taken as the difference in NO_3^--N content. These amounts were divided by the surface area of the tube to obtain results in g N m^{-2}.

In each of these samples soil moisture contents were determined by weighing soil samples after drying at 105 °C. Soil pH was measured after extracting 10 g field moist soil with 50 ml 1 *N* KCl.

Plant biomass and species composition

On 6 August 1991 a square of 50 by 50 cm was laid out in each of the 20 subplots in which all plants were clipped off flush with the ground. The harvested plants were separated per species into living and dead parts and into stems and non-woody parts. Roots were collected from 7 cm diameter soil samples taken to a depth of 10 cm and between 10 and 20 cm. These soil columns were washed out and thereafter roots were cleaned carefully from adhering soil particles. It proved impossible to distinguish between dead and living roots or between the roots of different plant species The harvested materials were weighed after drying at 70 °C. Nitrogen concentrations were measured with a Heraeus CHN-RAPID elemental analyser.

Statistical analysis

An one-way ANOVA was carried out to analyse site effects on amounts of soil organic matter, N mineralization and plant biomass. Differences between means were tested *a posteriori* using the Student–Newman–Keuls test. For this analysis we used the average of the two values of the N mineralization rate that were measured within each replicated subplot.

Results

Soil organic matter and N mineralization

During succession, soil organic matter accumulated rapidly (Figure 1). The amounts of organic matter and nitrogen in the FH layer and in the mineral layer were corrected for the total amounts of roots which were extracted from these layers. About 90% of the dead material had accumulated in the FH layer. Site effects on the quantities of dead organic matter and nitrogen in the FH layer are highly significant ($P < 0.001$). The quantities of organic matter and nitrogen in the litter layer are only significantly different when the two younger sites are compared with the two older ones ($P < 0.05$). There were no significant site effects on the amount of organic matter or nitrogen in the mineral layer. The decline during the later phases is an artefact of the sampling method used which resulted in a reduced thickness of the sampled mineral layer because of an increase in the thickness of the organic layer. The depth of the FH layer increased from 0, to respectively 2.6, 7.0 and 9.7 cm in the 1, 5, 35 and 76 year-old site.

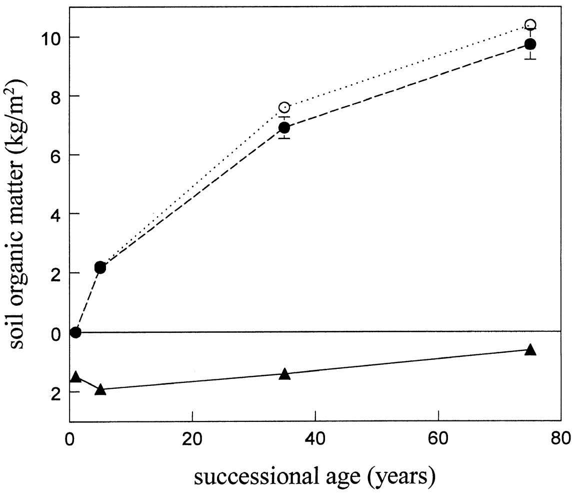

Figure 1. Amounts of organic matter per unit area in the L layer, the FH layer and the mineral layer to a depth of 20 cm versus successional age ($n = 5$). Bars indicate standard errors (note that some s.e. values are too small to be visible). Triangles: mineral layer; filled circles: FH-layer; open circles: L-layer + FH-layer.

The increase in the amount of dead organic matter did not have a clear effect upon volumetric soil moisture contents (Figure 2). We found no significant site effects on any of the sampling dates. Soil moisture levels were relatively high, which is probably why the increasing amount of soil organic matter had no effect upon the soil moisture content. The accumulation of soil organic matter did, however, have a strong impact on the soil acidity. The pH-KCl in the upper 10 cm declined from 6.8 immediately after turf removal to 4.4 in the oldest site (Figure 3).

The annual N mineralization was extremely low in all plots except at the 1990 site (Figure 4). Going from the 5-year-old site to the 76-year-old site, the N mineralization raised significantly from 0.2 to 0.8 g N m^{-2} yr^{-1}. Mineralization rates in all sites differed significantly from each other ($P < 0.05$), except between the 1986 and the 1957 sites. Net nitrification was only measurable in the 1990 plot. Here about 40% of the ammonium produced was oxidized to nitrate.

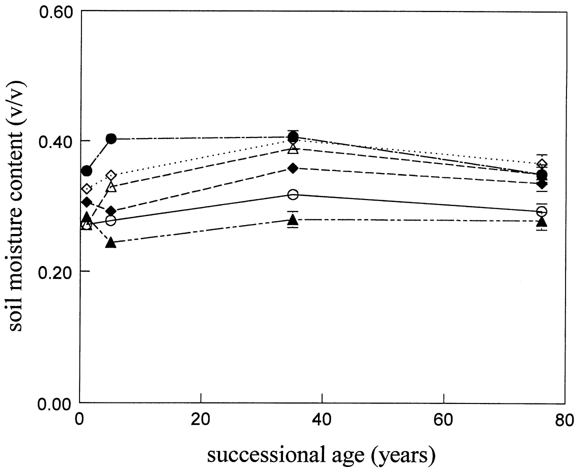

Figure 2. Volumetric soil moisture contents in the upper 10 cm on six different dates, versus successional age (n=10). Bars indicate standard errors (note that some s.e. values are too small to be visible). Open circles: 29 October 1991; open triangles: 21 January 1992; open squares: 17 March 1992; filled circles: 11 May 1992; filled triangles: 7 July 1992; filled squares: 1 September 1992.

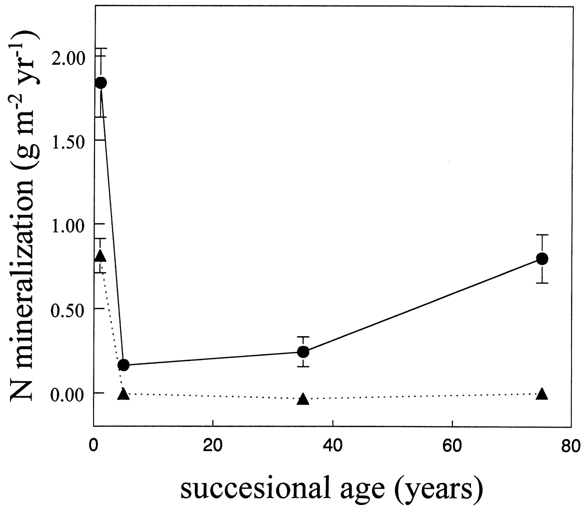

Figure 4. The annual nitrogen mineralization and nitrification rate versus successional age (n=10). Bars indicate standard errors (note that some s.e. values are too small to be visible). Triangles: nitrification rate; circles: mineralization rate.

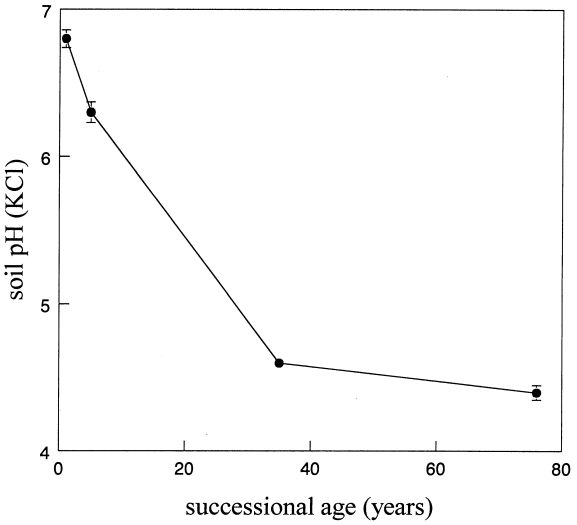

Figure 3. The pH-KCl in the the upper 10 cm of the soil versus successional age (n=10). Bars indicate standard errors (note that some s.e. values are too small to be visible).

Plant biomass and species composition

Above-ground plant biomass increased slowly during succession (Figure 5). In the 5-year-old plot the living above-ground biomass of vascular plants was only 150 g/m^2, but in the 76 year-old-plot it had increased to 1344 g m^{-2}. In the two older plots ca. 60% of the above-ground biomass consisted of woody stems. The harvested root biomass (including both living and dead roots) increased much more rapidly: from 830 g m^{-2} during the first year after turf removal to 3730 g m^{-2} after 35 years. The increase in total above-ground biomass and in root biomass was strongly significant ($P < 0.001$), except between 35 and 76 years.

The one-year-old site was only sparsely vegetated. On average, we recorded 2.8 ($\pm$ 0.4 s.e.) vascular plant species per subplot of 0.25 m^2 here. In the 5-year-old plot the vascular plant species diversity had greatly increased to 18.0 ($\pm$ 0.9 s.e.) species. Several species characteristic of early successional dune slacks were present here, such as *Schoenus nigicricans*, *Samolus valerandi*, *Radiola linoides*, *Pyrola rotundifolia*, *Littorella uniflora*, *Carex flacca* and *C. oederi* (Table 1). In these plots a large biomass of (mainly pleurocarpic) mosses was measured. In the older plots these mosses had almost disappeared. After 35 years the species composition had changed completely. In the 1956 plot the vegetation was dominated by the dwarf shrubs *Oxycoccus macrocarpos*, *Erica tetralix* and *Salix repens*. Species diversity had declined to 11.6 ($\pm$0.7 s.e.) species in this phase, but in the 76-year-old plot it had declined further to 8.0 ($\pm$0.3) species per 0.25 m^{-2}. In this oldest plot a shrub vegetation in which *Salix repens* seemed to be strongly dominant had developed. The biomass measurements, however, showed that the biomass of *Oxycoccus macrocarpos* was even higher, but this species was mainly present in the understorey below the *Salix* canopy. The average vegetation height had increased from ca. 50 cm in the 35-year-old plots to ca. 80 cm in the oldest

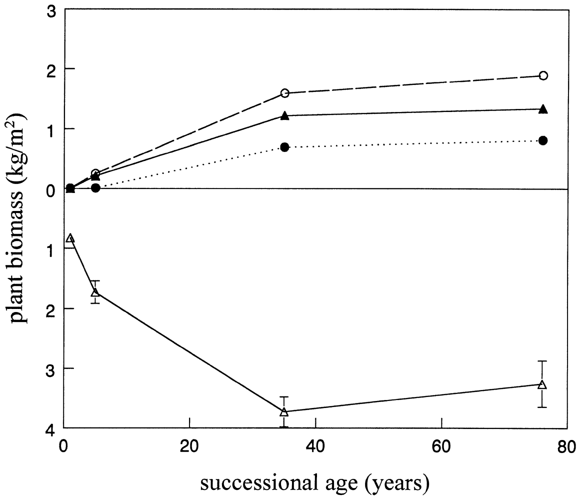

Figure 5. Dry weights per unit area of total root biomass, living woody stem biomass, living leaf biomass (including other non-woody organs) and standing dead material versus successional age (n=5). Bars indicate standard errors (some s.e. values are too small to be visible). Open triangles: root biomass; filled circles: stem biomass; filled triangles: leaf biomass + stem biomass; open circles: standing dead material + total living biomass.

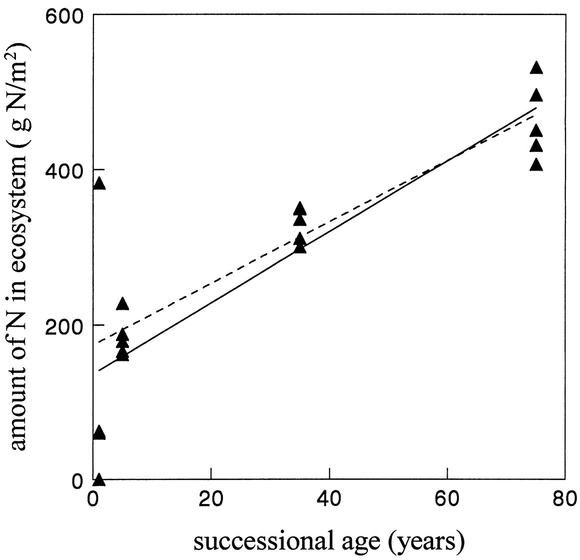

Figure 6. Total quantities of nitrogen in the whole ecosystem in living and dead plant mass and in the soil to a depth of 20 cm versus successional age. Solid line: regression includes all data points, slope = 4.6 g N m^{-2} yr^{-1}; dashed line: regression does not include data points of the 1-year-old site, slope = 4.0 g m^{-2} yr^{-1}.

site. Four vascular plant species increase systematically and significantly in biomass throughout the successional sequence: *Carex nigra, Calamagrostis epigejos, Oxycoccus macrocarpos* and *Salix repens*. *Salix* seedlings were observed in all the subplots of the 1990 site. After 76 years, accumulation of stem biomass had resulted in *Salix*-dominated shrublands in most of the study area.

Discussion

Reconstructing succession by a comparative study of neighbouring ecosystems which have developed during different time intervals is a risky enterprise, and should only be attempted if mineral substrate, groundwater level and climatological conditions are similar at all sites. In our study all sites were located within a relatively small area (7500 m^2) and the substrate consisted of homogeneous aeolean sand deposits. Spatial heterogeneity within the study area was mainly caused by variation in microrelief, but measurements of altitude and groundwater level did not show significant differences between the plots. Nevertheless, we have to emphasize that the five subplots within each site were pseudoreplicates and that – formally – no statistical distinction can be made between site effects and effects of successional age. Another important problem interpreting the results of such comparative studies is that the different sites have developed during different time periods and for this reason experienced different environmental conditions (such as atmospheric N deposition and CO_2 level) during the different phases of succession.

In an earlier study of succession in heathlands we found that the amount of nitrogen in the whole ecosystem (vegetation and soil) increased linearly during the first 30 years, when ericaceous dwarf shrubs were dominant (Berendse 1990). The slope of the regression line was about 3.1 g N m^{-2} yr^{-1}, which is close to the average N input through atmospheric deposition during the 30-year period considered. The total amounts of nitrogen in the dune valley ecosystems that we analysed seem to increase almost linearly too, although the large variation in the 1990 plot slightly obscures this relationship (Figure 6). Excluding the youngest plots the slope of the line is 4 g m^{-2} yr^{-1}, compared with 4.6 g m^{-2} yr^{-1} if these subplots are included. The total nitrogen input through atmospheric deposition in coastal dunes in the Netherlands is estimated to be at maximum 4.4 g m^{-2} yr^{-1} (Stuyfzand 1993). These values suggest that all nitrogen that enters the ecosystem is preserved, and losses due to nitrate leaching or denitrification are negligible.

Table 1. Biomass (g m^{-2}) of plant species in the four successional phases. Different letters within rows indicate significant differences between sites ($p < 0.05$).

Successional age (yr)	1	5	35	76
Agrostis stolonifera	+[a]	9[b]		
Carex oederi	+[a]	12[b]	1[a]	
Carex flacca		+		
Carex panicea		3	5	11
Carex nigra/trinervis			17[a]	36[b]
Calamagrostis epigejos		1[a]	26[a]	77[b]
Danthonia decumbens			2	
Erica tetralix (stems)			169	
Erica tetralix (leaves)			107	
Epipactis palustris			2	
Equisetum palustre	+	+		1
Eleocharis palustris				+
Empetrum nigrum (stems)		+		
Empetrum nigrum (leaves)		+		
Glaux maritima		+		
Hydrocotile vulgaris	+[a]	2[b]	+[a]	+[a]
Hippophae rhamnoides (stems)		+		
Hippophae rhamnoides (leaves)		+		
Galium palustre		+	+	+
Juncus alpino-articulatus/articulatus	2[a]	24[b]	+[a]	
Littorella uniflora		+		
Lythrum salicaria		43[a]	9[b]	
Lotus corniculatus			3	
Mentha aquatica		+[a]	+[b]	
Molinia caerulea			+	
Oxycoccus macrocarpos (stems)		+[a]	418[b]	444[b]
Oxycoccus macrocarpos (leaves)		1[a]	316[b]	310[b]
Ophioglossum vulgatum		+		+
Potentilla anserina		1	3	4
Prunella vulgaris	+			
Pyrola rotundifolia		+		
Ranunculus flammula	+	+	+	
Radiola linoides		+		
Salix repens (stems)	+[a]	8[a]	107[b]	371[c]
Salix repens (leaves)	+a	8[a]	34[b]	90[c]
Schoenus nigricans		37		
Samolus valerandi		+		
Trifolium fragiferum		+	+	
Musci		208[a]	1[b]	1[b]
Total living biomass	2[a]	358[b]	1222[c]	1345[d]

+: biomass < 0.5 g m^{-2}.

About 10% of the nitrogen that accumulates in the ecosystems studied is present in living plant biomass, whereas about 90% is stored in dead organic matter in the soil where most of it accumulates in the FH layer. This percentage is a minimum estimate, since we were unable to distinguish between living and dead roots. In this study, the proportion of nitrogen sequestered in the soil organic matter is larger than that in other ecosystems that we have studied in the Netherlands. In 30-year-old dwarf shrub-dominated heathlands and 120-year-old pine forests on inland dunes we found that ca. 80% of the amount of nitrogen in the ecosystem was present in the soil organic matter (Berendse 1990, 1998). Organic nitrogen is able to accumulate in the soil in such large amounts because in these ecosystems the litter decay rates are low relative to the turnover rates of plant biomass (Berendse et al. 1989). The nitrogen mineralization rates that we measured in the study described here are relatively high in the youngest plot (probably because of the decomposition of fresh roots remaining after turf stripping), but are extremely low in the three older plots. Here the N mineralization increased from 0.2 g N m^{-2} yr^{-1} after 5 years to 0.8 g N m^{-2} yr^{-1} after 76 years. For comparison, during heathland succession the N mineralization increased from 1 to 13 g m^{-2} yr^{-1} within 50 years and during succession in inland dunes it increased from 1 to 17 g m^{-2} yr^{-1} within 43 years. The low mineralization rates in coastal dune slacks may be the results of microbial activity being greatly reduced in the frequently waterlogged and hence anaerobic soils. Alternatively, some of the ammonium that accumulated in the incubated tubes may have been oxidized to nitrate, which was subsequently lost through denitrification. The accumulation of ammonium in incubated tubes due to the exclusion of plant uptake frequently results in an increased growth and activity of nitrifying bacteria. It is, however, questionable whether such losses are also significant in the undisturbed soil, where ammonium concentrations are kept at low levels by continuous plant uptake. Furthermore, the calculated whole ecosystem N accumulation rate (4.0–4.6 g m^{-2} yr^{-1}) also suggests that nitrogen losses are not quantitatively significant.

The great plant species diversity that we observed in the 5-year-old plot is characteristic of the early successional phases in wet dune slacks and frequently declines during the later phases (Grootjans et al. 1988; Ernst et al. 1996). It seems that many plant species readily germinate and establish on the bare soil in the first few years. After 35 years a litter layer had developed and the above-ground vascular plant biomass had increased more than 8-fold from 156 to 1221 g m^{-2}. Such changes hamper the establishment of species for reasons including the strong reduction of the light intensities reaching seeds and seedlings. Moreover, competition for light due to the accumulation of above-ground biomass in the woody dwarf shrub species and the resulting increase in vegetation height caused many short plant species characteristic of the diverse early phases to disappear. In heathlands the strong increase in N mineralization caused the above-ground productivity to rise approximately 6-fold which strongly favoured the perennial grasses that subsequently replaced the ericaceous dwarf shrubs. Fertilization experiments with factorial combinations of N, P and K in each of the four sites in our dune slack area showed that N and P were limiting plant productivity in the youngest site, whereas only N limited plant growth in the three older phases (E. J. Lammerts, unpublished results). N fertilization had also significant effects upon species composition, resulting in an increase in *Juncus alpino-articulatus* in the youngest site and an increase in *Calamagrostis epigejos* in the older plots. In this fertilization experiment 16 g N m^{-2} (as slow release granules) was applied at the beginning of the growing season. However, the increase in N mineralization which we measured in the dune valley chronosequence seems too small to have an important impact upon the species composition.

Another important effect of the accumulation of soil organic matter is the change in pH in the upper soil layer, which declined by more than two units. Soil acidification may have an important negative effect upon the germination of many plant species, but it is also possible that the declining pH reduced the vitality of adult plants of species such as *Schoenus nigricans*. In our sequence this species only occurred in the 5-year-old plots, but in another Dutch coastal dune area where calcium contents in the soil were much higher, *Schoenus* was still one of the dominant species after 57 years (Ernst et al. 1996). Soil organic matter accumulation in the plots studied by Ernst and colleagues seemed to be similar to that in our study area, but above-ground biomass had increased more slowly (950 g m^{-2} after 57 years as compared to 1222 g m^{-2} after 35 years in our sequence) probably because woody shrub species were less frequent. They found that the perennial grass *Calamagrostis epigejos* had expanded from 40% of the total above-ground biomass after 17 years to 68% after 57 years, whereas in this period *Schoenus* had declined from 49% to 26%.

In conclusion, we postulate that most of the changes in species composition in our study area occurred due the accumulation of biomass in the woody species such as the ericaceous dwarf shrubs and *Salix repens* and not due to the increase in N mineralization as we had observed in inland heathlands. Almost all the species established during the first few years after turf removal. All the species found in the old plots and not in the younger plots appeared to be present in the younger sites outside the harvested subplots. After 76 years, *Salix repens* seedlings that were presumably already present during the first year had grown into mature shrubs that completely dominated the upper canopy of the vegetation. Competition for light resulted in the extinction of almost all the short plant species. Only non-woody species that are able to reach greater plant heights such as *Calamagrostis epigejos* and *Carex nigra* were able to maintain themselves or even to expand further.

References

Berendse, F., Bobbink, R. and Rouwenhorst G. A. 1989. A comparative study on nutrient cycling in wet heathland ecosystems. II. Litter decomposition and nutrient mineralization. Oecologia 78: 338–348.

Berendse, F. 1990. Organic matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. J. Ecol. 78: 413–427.

Berendse, F. 1998. Effects of dominant plant species on soils during succession in nutrient-poor ecosystems. Biogeochemistry (in press).

Berendse, F. and Elberse W. T. 1990. Competition and nutrient availability in heathland and grassland ecosystems. pp. 93–115. In: J. Grace and D. Tilman (eds.), Perspectives on Plant Competition. Academic Press, Orlando.

Berendse, F., Schmitz M. and De Visser W. 1994. Experimental manipulation of succession in heathland ecosystems. Oecologia 100: 38–44.

Crocker, R. L. and Major J. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J. Ecol. 43: 427–448.

Ernst, W., Slings, Q.L. and Nelissen, H. J. M. (1996). Pedogenesis in coastal wet dune slacks after sod-cutting in relation to revegetation. Plant Soil 180: 219–230.

Grootjans, A. P., Hendriksma P., Engelmoer M., and Westhoff, V. 1988. Vegetation dynamics in a wet dune slack. I. Rare species decline on the Wadden island of Schiermonnikoog in the Netherlands. Act. Bot. Neerl. 37: 265–278.

Olson, J. S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. Bot. Gaz. 119 (3): 125–170.

Stuyfzand, P. J. 1993. Hydrochemistry and hydrology of the coastal dune area of the Western Netherlands. Ph.D. Thesis, Free University Amsterdam.

Tilman, D. 1988. Plant strategy and the dynamics and structure of plant communities. Princeton University Press, Princeton, NJ.

Van Dieren, J. W. 1934. Organogene Dunenbildung, einen geomorphologische Analyse der westfriesischen Insel Terschelling mit pflanzensoziologischen Methoden. Nijhoff, Den Haag.

Westhoff, V. and Van Oosten, M. F. 1991. De plantengroei van de Waddeneilanden. KNNV, Utrecht.